

## ON SOCIAL SINGLE SPECIES POPULATIONS

In all formal mathematical theories of population growth, population increase is considered to be limited by some function of the number of animals present. The classical Verhulst-Pearl equation of population growth can be written as:

$$\frac{dN}{dt} = rN \frac{(K - aN)}{K}, \quad (1)$$

where  $N$  is the number of organisms in the population,  $r$  the intrinsic rate of increase and  $K$  the size (in one sense) of the available universe.  $a$  is a proportionality constant.

Measuring the environment in terms of the number of organisms in the population implicitly assumes that there is something ( $x$ ) in the environment such that  $\frac{a}{K}$  of  $x$  is required by each animal at equilibrium. If the total available quantity of  $x$  increases in the environment the equilibrium number of organisms in the population increases proportionally.

In effect, the amount of  $x$  required by each organism in the population is independent of the other organisms in the population while the amount of  $x$  available to each organism is dependent on the total amount available in the environment and on the number of organisms competing for it.

This relation is diagrammed in Figure 2a where the  $I_i$  represent individual animals of the population,  $x$  the amount of material in the environment, and the pairs of arrows represent the demands of the individuals on the total quantity

of  $x$  and the amount of  $x$  which each individual actually obtains.

The Verhulst-Pearl population equation has been amplified to include two species and the competitive interaction between them (Gause 1935).

Hutchinson (1947) has suggested that certain species-competition situations can be adequately described only by assuming a social interaction between members of each species. This situation is formulated as:

$$\left. \begin{aligned} \frac{dN_1}{dt} &= r_1 N_1 \frac{(K_1 - a_1 N_1 - \gamma N_2^2)}{K_1} \\ \frac{dN_2}{dt} &= r_2 N_2 \frac{(K_2 - a_2 N_2 - \delta N_1^2)}{K_2} \end{aligned} \right\} \quad (2)$$

where the subscripts 1 and 2 refer to species one and two respectively.  $K$ ,  $N$ , and  $r$  retain their previous definition.

$\gamma N_2^2$  and  $\delta N_1^2$  express the depressing effect of each species on the population of the competing species. The effectiveness of each species in its interaction with the competing species is directly proportional to the interaction between the individuals of the species.

This is a simple type of social interaction. Hutchinson points out that this is a simple example of a more general case in which  $\gamma N_2^2$  and  $\delta N_1^2$  are replaced by the power series:

$$\left. \begin{aligned} \alpha N_2, \quad \gamma N_2^2, \dots \\ \beta N_1, \quad \delta N_1^2, \dots \end{aligned} \right\} \quad (3)$$

Some interesting conclusions can be derived if a similar notation is used to describe social interactions in single-species population growth. Consider the case:

$$\frac{dN}{dt} = rN \frac{(K - bN^2)}{K}. \quad (4)$$

In the initial non-social case (1), the relation between size of the environment (measured as amount of  $x$ ) and number of animals at the upper asymptote could be written as:

$$K - aN = 0 \quad (5)$$

while in the simple social case (4), it becomes:

$$K - bN^2 = 0 \quad (6)$$

while in the most general case it becomes:

$$K - f(N) = 0 \quad (7)$$

where  $f(N)$  may be a power series.

We define the efficiency of an asymptotic population as  $\frac{K}{N}$ , that is, as the number of organisms which can be maintained by a unit of environment.

We define the instability of the population as  $\frac{dN}{dK}$ , that is, as the rate of change of population size with size of the environment.

Comparing the situations represented by (5) and (6) we find that for all sufficiently high values of  $N$ , taking equal values of  $K$ , both efficiency and instability are higher in the non-social case, regardless of the absolute values of  $a$  and  $b$ , which must however be positive.

If negative values of the coefficients in (5) and (6) were permitted, the population would increase with negative environmental size, which is absurd.

The relation between number of individuals in the population at its upper asymptote and the of the environment ( $K$ ) is shown in Figure 1 for social and non-social situations.

If the proportionality constants  $a$  and  $b$  are considered equal then the efficiency and instability of a social population are always lower than those of a non-social population.

Taking (7) as a power series, (5) and (6) can be considered as representing those special cases in which the first and second coefficients respectively are the only non-zero coefficients in

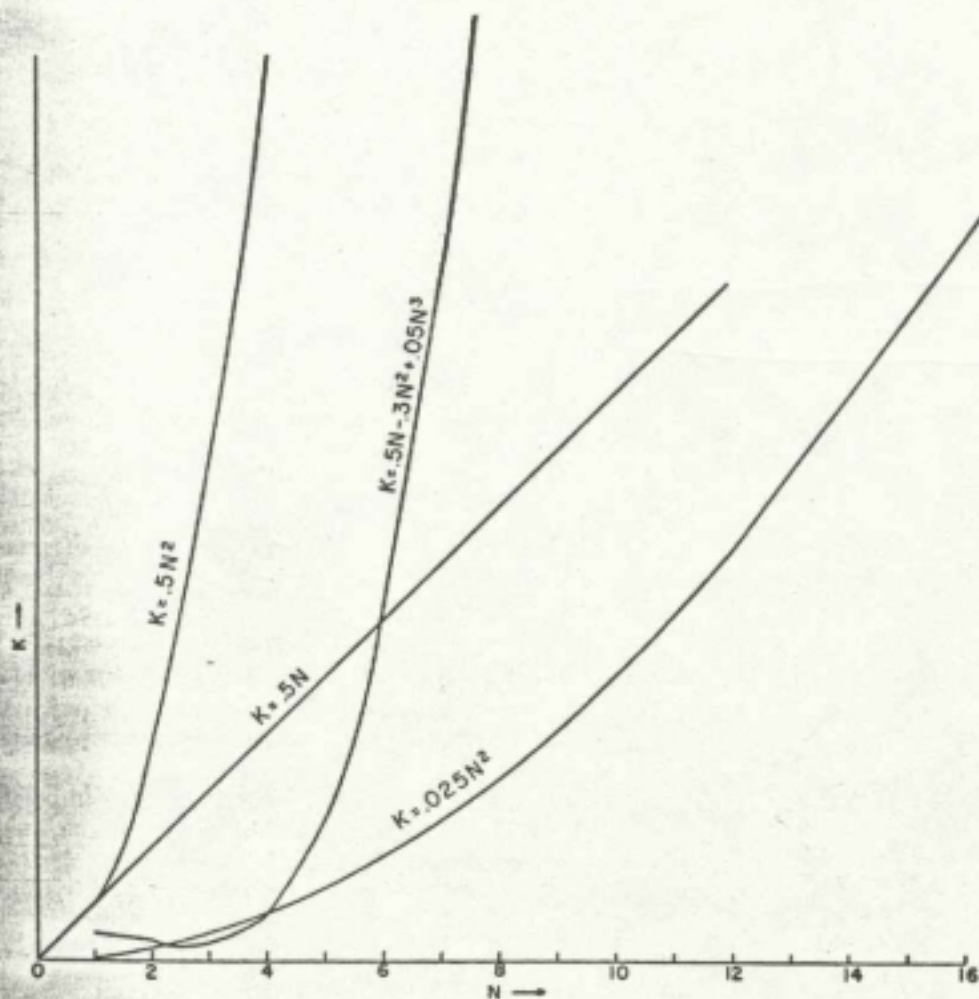


FIG. 1.



the series. Consider two closely related populations, one of which has a genetic tendency to follow (5) and the other (6). There is no *a priori* reason to consider the coefficients  $a$  and  $b$  equal. If, however,  $a$  is equal to  $b$ , the social population will show a lower efficiency and lower instability than the non-social population for all values of  $N$ . If  $b < a$  then there will be an apparent "optimal density" effect when the two populations are compared. For sufficiently low values of  $N$  the social population will show a higher efficiency than the non-social population, but since the efficiency of the social population will decrease monotonically with  $K$  and  $N$  this does not constitute a true "optimal density" effect.

It seems advisable to limit the term "optimal density" to those situations in which the efficiency of a single population over some range of values of  $N$  is higher than that at either a lower or higher density value.

Optimal density can be discussed in this formulation in terms of the first three members of a

power series:

$$aN, bN^2, cN^3 \dots \quad (8)$$

The biological significance of the first three members of the series seems fairly clear. The expression  $aN$  refers to competition between individuals of the population for some material in the environment, disregarding all direct interactions between individuals. The term  $bN^2$  refers to direct interaction between the individuals of the population, dependent on population density and independent of the environment, except in so far as this interaction affects the competition for environmental material between organisms. This is indicated in Figure 2b by uniting all the individuals of the population in a box, to indicate their interaction and drawing arrows to indicate the effect of this interaction on the competitive process.

The third-order term may represent the effect of groups of individuals on single individuals; for example, the effect of neighboring bands of monkeys on an individual monkey of one band or the effect of other family groups.

This is schematized as Figure 2c where the bracket groups the population into the system  $P$  which in turn affects each individual  $I_i$ .

The significance of higher members of the power series seems vague at present.

Taking a population which follows the form

$$K - aN - bN^2 - cN^3 = 0$$

a true optimal-density effect which does not violate previous considerations of possibility can result if, and only if,

- a)  $b$  is negative
- b)  $b < a$

and

- c)  $b > c$

with  $a$  and  $c$  positive.

The relation between the coefficients is further restricted by the requirement that  $N$  and  $K$  must be positive and greater than zero. This restriction limits the relation between  $a$ ,  $b$ , and  $c$  in a relatively stringent way. It has been found arithmetically that values of  $b$  which will produce an optimal-density effect without violating the conditions of  $K$  and  $N$  being positive will bear the relation shown in Figure 3 to  $a$ , with  $c$  taken as unity.

Optimal-density effects are impossible if  $a < 2c$ . For values of  $b$  above the values in the striped area of Figure 3 there exists a positive value of  $N$  for which  $K$  is negative. For values of  $b$  below this area efficiency decreases monotonically with  $N$ , so that no optimal-density effect is observed.

The maximal optimal-density effect is found in the range of  $N = 2$  at  $a = 3c$  to  $N = 9$  at  $a$

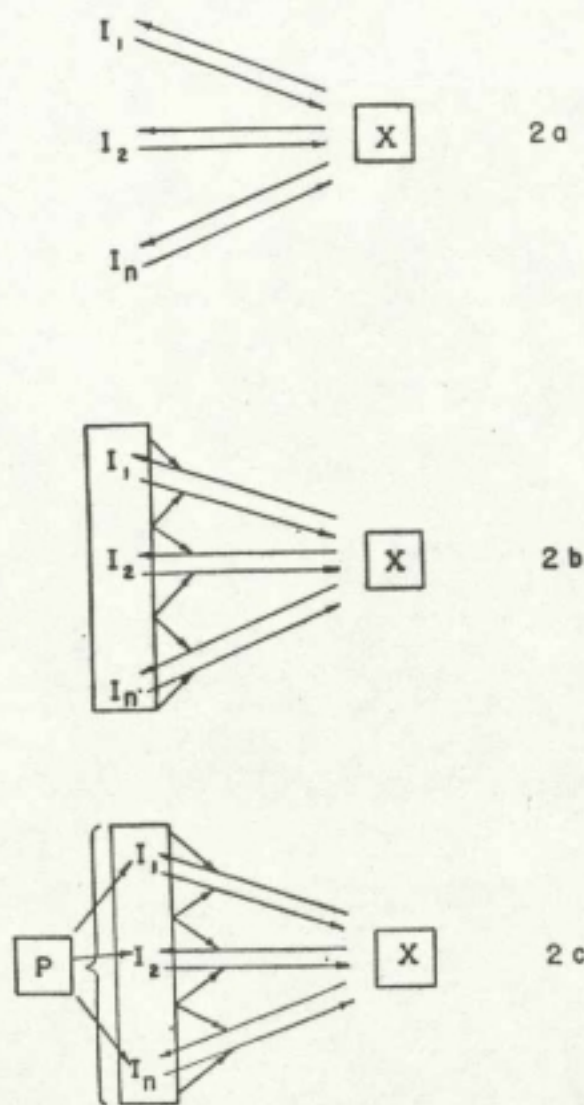


FIG. 2.

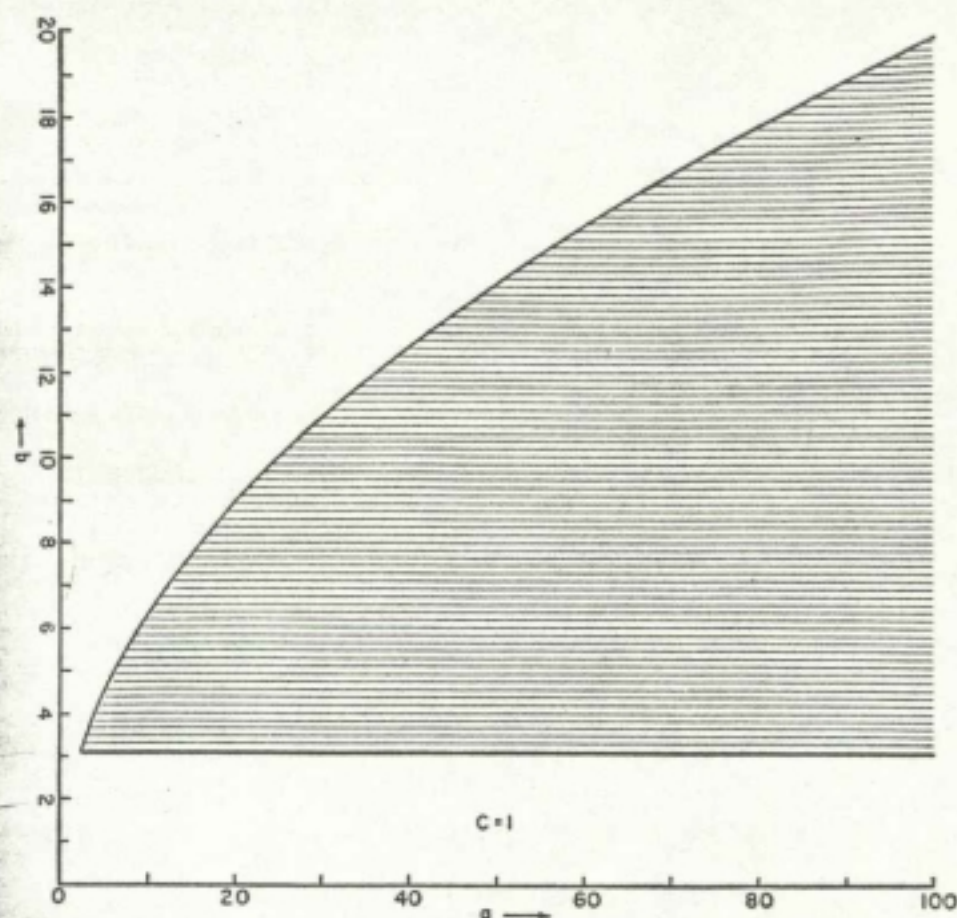


FIG. 3.

$\approx 1000 c$ . This is in surprisingly close agreement with the values reported for three experimental situations in which optimal density was measured.

In *Tribolium confusum* MacLagen (1932) and Chapman (1928) found that maximal reproduction per female occurred when two to four beetles were placed in each experimental container. Pratt (1943) found maximal longevity in *Daphnia magna* females at a density of five females in each 100 cc container of culture medium. Vetulani (1931) found maximal growth rates in mice raised two to four to a cage at 16° C. Other reported instances of optimal density effects do not seem so well substantiated as these three (see Allee *et al.* 1949). The significance of the agreement with the predicted optimal density level is not clear since so many simplifications have been introduced into the theory.

It should be made clear that the concept of population density has been used as an absolute number throughout this discussion. No restriction has been made on the geometric size of the environment except that it be sufficiently small to permit continual interaction between the organisms of the population. The consider-

ation of population density as an absolute number is implicit in the common use of the term  $\frac{K - aN}{K}$  in (1).

The form of Figures 1 and 3 is independent of the implicit assumptions of the Verhulst-Pearl equation. If the population consisted of a series of non-equivalent classes of animals (as in the formulations of Leslie 1948 and Slobodkin 1953), instead of the single class implicit in  $N$ , the same results would follow, if the number of animals in each category remained constant.

The system is probably completely inapplicable in any situation in which communication occurs between animals, as in bees. In such a situation the value of  $K$  is in a sense determined by the activity of the organisms.

Figure 1 is probably of significance as an indication of the environmental conditions which would permit social systems to evolve.

If the population exists in a highly variable environment there may be a selective advantage in developing higher-order interactions between organisms to provide stability at the cost of efficiency. Efficiency becomes of primary significance in relatively stable environments.



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## SUMMARY

Application of Hutchinson's (1947) notation for social interaction in an inter-species competition situation to the growth of single species populations permits the derivation of general conditions for the occurrence of optimal density effects in asymptotic populations.

If the relation between  $K$  (the "size" of the environment) and  $N$  (the number of animals at population equilibrium) is expressed as

$$K = aN + bN^2 + cN^3,$$

where  $a, b, c$  are constants, optimal density effects will be found whenever the ratio  $a:b:c$  is such as to lie in the shaded portion of Figure 3.

In general, social populations have a lower efficiency and higher stability than non-social populations.

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THE BALANOID BIOME-TYPE OF INTERTIDAL ROCKY SHORES<sup>1</sup>

The concept of the biome and the biome-type has arisen entirely from studies of terrestrial ecology. Several other terms are partial or almost direct synonyms of these expressions; however, all point toward common ecological principles that, in my opinion, are best represented by the biome-type as recently defined and discussed by Allee, Emerson, Park, Park and Schmidt (1949).

Though biome-types are evident on land in relationships between climate, physiography and biotic development, attempts to demonstrate comparable ecological principles in other environments have not been convincing nor have they been widely accepted. Clements and Shelford (1939) suggested that certain specific marine communities be recognized as having the ecological status of a biome. Their Balanus-Littorina Biome suggested this type of ecological relationship in the intertidal zone. With qualifications in the light of later studies, particularly the work of Stephenson and Stephenson (1949) who recognize a balanoid mid-

littoral zone, the biome status of intertidal rocky shores can be further clarified. Though generally regarded as marine, intertidal areas are neither terrestrial nor oceanic; thus to regard a biotic development in these levels as a biome does not preclude other interpretations of submarine environments, such as proposed by Allee *et al.* (1949) to the effect that in the oceans we are dealing with a complex to be regarded as a single biome-type.

More specifically the Balanus-Littorina community of the North Pacific was singled out by Clements and Shelford for identification as a biome. They noted that their acquaintance with it is primarily in the Puget Sound area but pointed out that, though the biome is a band only a few feet high limited to the intertidal zone, "... it is apparently widely distributed around the North Pacific." These authors mentioned as dominant in this community three species of barnacles, *Balanus cariosus*, *B. glandula*, and *Chthamalus dalli*, and two species of mussels, *Mytilus edulis* and *M. californianus*. As the most characteristic motile forms they mentioned three littorine gastropods, *Littorina sitchana*, *L. scutulata* and

<sup>1</sup>Contribution No. 16, Oceanographic Institute, Florida State University.